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Mangrove forests in a rapidly changing world: Global change impacts and conservation opportunities along the Gulf of Mexico coast

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A B S T R A C T

Mangrove forests are highly-productive intertidal wetlands that support many ecosystem goods and services. In addition to providing fish and wildlife habitat, mangrove forests improve water quality, provide seafood, reduce coastal erosion, supply forest products, support coastal food webs, minimize flooding impacts, and support high rates of carbon sequestration. Despite their tremendous societal value, mangrove forests are threatened by many aspects of global change. Here, we examine the effects of global change on mangrove forests along the Gulf of Mexico coast, which is a valuable region for advancing understanding of global change impacts because the region spans multiple ecologically-relevant abiotic gradients that are representative of other mangrove transition zones across the world. We consider the historical and anticipated future responses of mangrove forests to the following aspects of global change: temperature change, precipitation change, accelerated sea-level rise, tropical cyclone intensification, elevated atmospheric carbon dioxide, eutrophication, invasive non-native species, and land use change. For each global change factor, we provide an initial global perspective but focus primarily on the three countries that border the Gulf of Mexico: United States, Mexico, and Cuba. The interactive effects of global change can have large ecological consequences, and we provide examples that highlight their importance. While some interactions between global change drivers can lead to mangrove mortality and loss, others can lead to mangrove expansion at the expense of other ecosystems. Finally, we discuss strategies for using restoration and conservation to maximize the adaptive capacity of mangrove forests to global change. To ensure that the ecosystem goods and services provided by mangrove forests continue to be available for future generations, there is a pressing need to better protect, manage, and restore mangrove forests as well as the adjacent ecosystems that provide opportunities for adaptation in response to global change.

1. Introduction

Mangrove forests are intertidal wetlands found along sheltered tropical and subtropical coasts (Tomlinson, 1986; Spalding et al., 2010; Twilley and Day, 2012; Rivera-Monroy et al., 2017). These highly-productive ecosystems provide many critical ecosystem goods and services. In addition to providing fish and wildlife habitat, mangrove forests reduce coastal erosion, provide seafood, improve water quality, supply forest products, support coastal food webs, minimize flooding impacts, and support high rates of carbon sequestration (Ewel et al., 1998; Barbier et al., 2011; Lee et al., 2014). Despite the tremendous societal value of mangrove forests, we live in an era of unprecedented

ecological change (Millennium Ecosystem Assessment, 2005; Crutzen, 2006) that has negatively affected mangrove forests in many parts of the world. In the past century, the rate of mangrove loss has been particularly high primarily due to direct conversion of mangrove forests to other land uses (FAO, 2007; Hamilton and Casey, 2016; Thomas et al., 2017). In the coming century, climate change, accelerated sea-level rise, and other aspect of global change will affect mangrove forests across the globe (Woodroffe, 1990; Gilman et al., 2008; McKee et al., 2012; Alongi, 2015; Asbridge et al., 2015; Ward et al., 2016; Castellanos-Galindo et al., 2017; Jennerjahn et al., 2017; Romañach et al., 2018). Historical records indicate that mangrove forests are highly resilient ecosystems that have the potential to adapt and adjust

to changing conditions (Woodroffe and Grindrod, 1991; Doyle et al., 2010; Krauss et al., 2014b; Woodroffe et al., 2016; Danielson et al., 2017). However, given the amount of change that has occurred in the recent past and is expected in the near future, there is a pressing need to better anticipate and prepare for the ecological consequences of global change.

The Gulf of Mexico is a valuable region for advancing understanding of global change impacts to mangrove forests because, in addition to a rich legacy of ecological research, coastal wetlands in the region are abundant and span multiple ecologically-relevant abiotic gradients (López-Portillo and Ezcurra, 2002; Méndez-Alonzo et al., 2008; Day et al., 2013; Yáñez-Arancibia et al., 2014; Hamilton and Casey, 2016). Mangrove forests, salt marshes, and salt flats are all different types of coastal wetlands that are common in the region, and ecological transitions between these three different kinds of coastal wetlands can be induced by global change factors. Coastal wetlands in the region span ecologically-relevant temperature and precipitation gradients (Osland et al., 2016; Gabler et al., 2017). Globally, there are many regions where coastal wetlands are governed primarily by a single climatic factor (e.g., either temperature or precipitation); however, there are fewer regions where coastal wetlands are governed simultaneously by two climatic factors (Osland et al., 2017b). The Gulf of Mexico's abundant wetlands also span diverse geomorphic gradients that modulate wetland responses to sea-level rise (Woodroffe, 2002); coastal wetlands in the region are located in large sediment-dependent deltas (e.g., Grijalva-Usumancinta, Mexico; Mississippi River, USA) and also along karst-dominated, sediment-poor oligotrophic coasts (e.g., Yucatan Peninsula, Mexico; Cuba; Everglades, USA). The combination of continuous wetland coverage and diverse abiotic gradients along the Gulf of Mexico coast provide globally-relevant opportunities for testing hypotheses of global change impacts to mangrove forests. Since the abiotic gradients present in the Gulf of Mexico are also influential in other regions of the world, global change insights derived from Gulf of Mexico coastal wetlands can advance understanding in other parts of the world.

Our review focuses on mangrove forests in the three countries that border the Gulf of Mexico: United States, Mexico, and Cuba. Our overarching aim is to synthesize understanding of the historical and anticipated future responses of Gulf of Mexico mangrove forests to temperature change, precipitation change, accelerated sea-level rise, tropical cyclone intensification, elevated atmospheric carbon dioxide, eutrophication, invasive non-native species, and land use change. The interactive effects of global change can have large ecological consequences, and we provide examples that highlight the relevance of such interactions. While some interactions between global change drivers can lead to mangrove mortality and loss (Duke et al., 2017;

Lovelock et al., 2017), other interactions can lead to mangrove expansion at the expense of other ecosystems (Table 1). Following our examination of global change impacts, we discuss strategies for using restoration and conservation to maximize the adaptive capacity of mangrove forests in the face of rapid global change.

2. Distribution and diversity

Climatic factors greatly influence the global distribution and diversity of mangrove forests (Woodroffe and Grindrod, 1991; Saenger, 2002; Duke, 2017) (Fig. 1). Across the globe, mangrove forests are, in general, most abundant, diverse, and productive in tropical wet climates (Figs. 1–2). Freezing and chilling temperatures can lead to mangrove mortality, loss of aboveground biomass, reduced productivity, and/or decreased reproduction (Duke, 1990; Stuart et al., 2007; Ross et al., 2009; Quisthoudt et al., 2012; Lovelock et al., 2016). Hence, minimum air temperature regimes limit the poleward distribution of mangrove forests on multiple continents (Figs. 1 and 3). In addition to temperature constraints, mangrove forests are also sensitive to hypersaline conditions that are most prevalent in areas with low precipitation and minimal freshwater inputs (Reef and Lovelock, 2014; Lovelock et al., 2016). Hypersaline edaphic conditions can develop as tidally-derived oceanic waters evaporate and the remaining salts become concentrated (Zedler, 1982; Castañeda-Moya et al., 2006; Lovelock et al., 2017). Along arid and semi-arid coastlines, hypersalinity and lack of precipitation can limit the distribution and diversity of mangrove forests (Bucher and Saenger, 1994; Saenger, 2002; Semeniuk, 2013) (Figs. 1 and 3).

In general, the species richness of mangroves in the western hemisphere (i.e., the Atlantic East Pacific biogeographic zone: North America, South America, and western Africa) is lower than in the eastern hemisphere (i.e., the Indo West Pacific biogeographic zone) (Duke, 2017). This is due primarily to historic and geographic factors that resulted in regional differences in the rate of origin of new mangrove lineages (Duke, 1992; Ricklefs and Latham, 1993; Duke et al., 1998; Ellison et al., 1999; Ricklefs et al., 2006) (Figs. 1 and 3). However, physiological constraints associated with freezing temperatures and hypersaline edaphic conditions result in species richness being highest in tropical wet climates. Hence, within each of the two major mangrove biogeographic zones, there are strong relationships between species richness and air temperature and rainfall regimes (Fig. 3).

The Gulf of Mexico contains two ecologically-relevant climatic gradients that greatly influence wetland ecosystem structure and function (Fig. 4 and Fig. 5) (Osland et al., 2016; Gabler et al., 2017). From south-to-north, the duration and frequency of winter air temperature extremes in the Gulf of Mexico control the distribution and

Table 1
Interactions between global change drivers can have large ecological consequences. In many cases, the interactive effects of multiple drivers are larger than the effects of a single driver. The examples below highlight the importance of considering interactive effects.

| Global change drivers	Ecological effect	Source(s)
↓ precipitation + ↓ sea level + ↑ temperature	Mortality	Lovelock et al., 2017, Duke et al., 2017
↓ precipitation + ↑ temperature	Altered biotic interactions	McKee et al., 2004
↑ atmospheric carbon dioxide + ↑ sea-level	Elevation change	Langley et al., 2009, Cherry et al., 2009
↑ atmospheric carbon dioxide + ↑ temperature	Expansion	Saintilan and Rogers, 2015
↓ freshwater input + ↑ sea-level + ↑ temperature	Expansion	Krauss et al., 2011, Howard et al., 2017
↓ freshwater input + ↓ precipitation + ↑ temperature	Mortality	Osland et al., 2014a, b
↑ nutrient + ↑ atmospheric carbon dioxide	Altered biotic interactions	McKee and Rooth 2008
↑ nutrient + ↑ sea-level + ↓ freshwater input	Altered productivity	Adame et al., 2013a, b
↑ sea-level + ↑ precipitation + ↑ freshwater input	Transgression	López-Medellín et al., 2011
↑ sea-level + ↑ tropical cyclone intensity	Transgression	Doyle et al., 2010; Smith et al., 1994
↑ temperature + ↑ tropical cyclone intensity	Range limit expansion	Osland et al., 2013
↑ low-lying, coastal development + ↑ sea-level	Coastal squeeze	Enwright et al., 2016
↑ invasive non-native species + ↑ sea-level	Delayed transgression	See invasive species section
↑ tropical cyclone intensity + ↑ sea-level	Structural change, Regime shift	Rivera-Monroy et al., 2011
↑ land use change + ↑ sea-level + ↓ freshwater input	Habitat loss	None
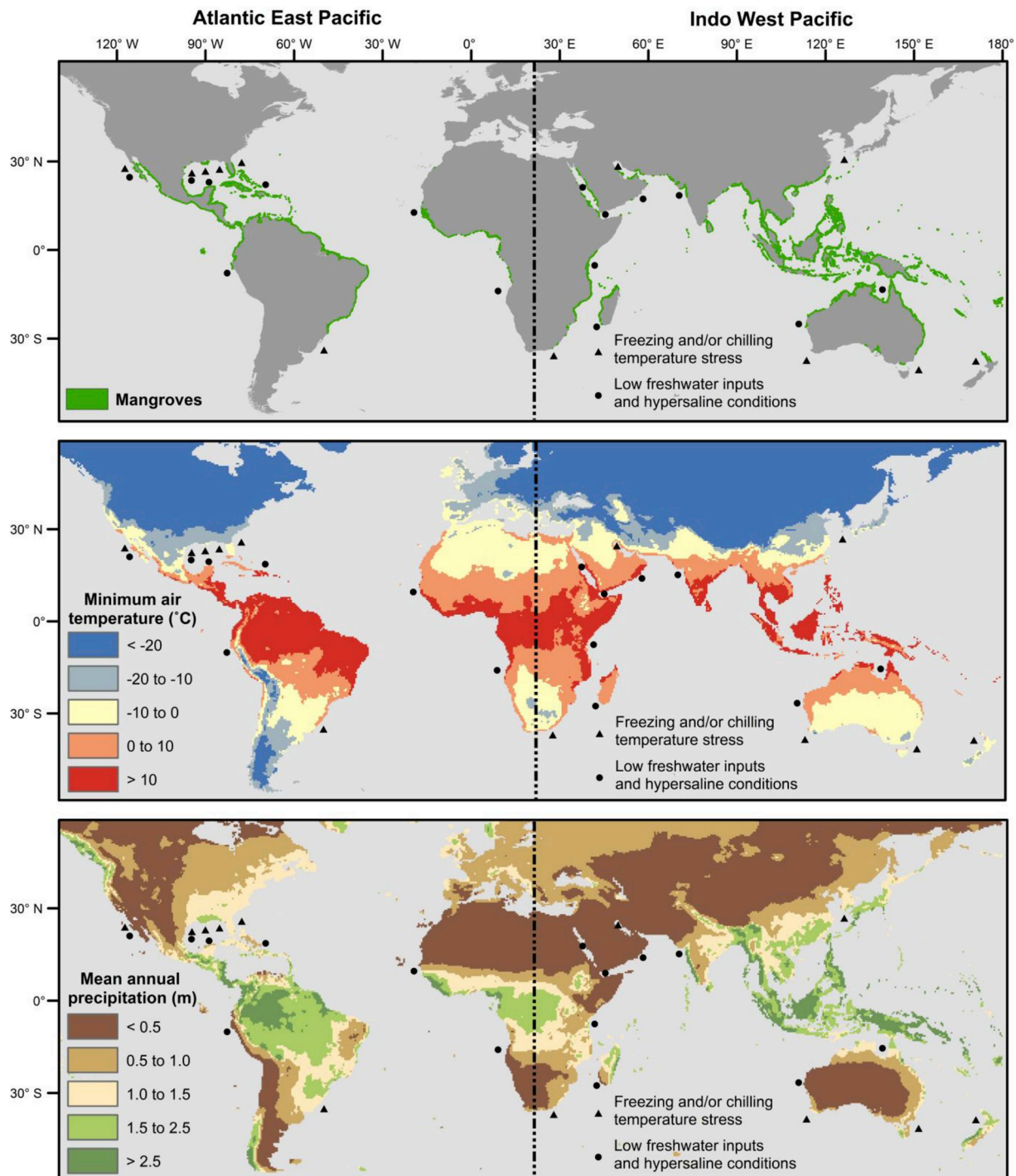
Fig. 1. Climatic factors control the global distribution of mangrove forests. Maps of: (upper) the global distribution of mangrove forests (Giri et al., 2011); (middle) minimum air temperature; and (lower) mean annual precipitation. Triangle and circle symbols are used to denote areas where minimum air temperature or mean annual precipitation play an especially important ecological role. The world is divided into two biogeographic zones, the Atlantic East Pacific and the Indo West Pacific (Duke, 2017). Figures and information adapted from Osland et al. (2017b).

diversity of mangrove forests and salt marshes (Osland et al., 2013; Cavanaugh et al., 2014). Near the United States-Mexico border and also near the tip of the Yucatán Peninsula, low precipitation, minimal freshwater inputs, and hypersaline edaphic conditions greatly influence mangrove forest and salt flat distribution and diversity (Figs. 4 and 5) (Osland et al., 2017b). Although air temperature appears to be the primary climatic factor that governs mangrove forests in the northeastern and eastern Gulf of Mexico, mangrove forests in the western and northwestern Gulf of Mexico are regulated by both precipitation and

winter air temperature regimes (Figs. 4 and 5) (Osland et al., 2017b).

Collectively, mangrove forests in the Gulf of Mexico are estimated to cover 6870 km², which represents about 8% of the total global mangrove cover. Mangrove cover along the Gulf of Mexico is highest in Mexico followed by the United States and Cuba (Table 2). Mangroves are abundant in Cuba (Menéndez Carrera and Guzmán Menéndez, 2006; Menéndez Carrera, 2013), which ranks fourteenth in the world in terms of mangrove cover with approximately 2% of the total global mangrove cover (Hamilton and Casey, 2016); however, the Gulf of

Fig. 2. Climatic factors control mangrove structure and function. Photos of: (upper left) *Rhizophora mangle* prop roots in Florida (USA), (upper right) *Avicennia germinans* pneumatophores in Florida (USA), (middle left) a microbial mat in a hypersaline flat without mangroves in Texas (USA), (middle right) a freeze-damaged *A. geminans* individual in Louisiana (USA), (bottom left and bottom right) mixed species mangrove forests in Veracruz (Mexico).

Mexico boundary used in this study only includes a small percentage of Cuba's total mangrove cover. The total mangrove cover in the Gulf of Mexico portion of Cuba is 473 km² (Menéndez Carrera, 2013), which represents about 7% of the total Gulf of Mexico mangrove cover (Table 2). Mangrove cover along Cuba's gulf coast is highest in the Pinar del Río Province (Table 2). For our geospatial analyses, we use Gulf of Mexico boundaries adapted from those presented by Felder et al. (2009) (Fig. 4, dashed lines in upper panel). To differentiate the Gulf of Mexico from the Caribbean Sea and Atlantic Ocean, we used a southern oceanic

boundary that extends from Cabo Catoche (Quintana Roo, Mexico) to Cabo de San Antonio (Pinar del Río, Cuba) and a southeastern oceanic boundary that extends from Key Largo (Florida, United States) to Bahía de Cárdenas (Matanzas, Cuba), respectively.

In Mexico, mangroves are abundant along most of the gulf coast states. However, low precipitation and hypersaline conditions limit the distribution of mangrove forests in the northern portion of the state of Tamaulipas, near the Mexico-United States border, and near the tip of the Yucatán Peninsula (Figs. 4 and 5; Table 2). The total mangrove cover along Mexico's gulf coast is estimated to be 3863 km², which represents 56% of the total Gulf of Mexico mangrove cover (Table 2) (CONABIO, 2016). Campeche and Yucatán are Mexico's gulf coast states with the highest mangrove cover (Table 2).

The total mangrove cover along the gulf coast of the United States is estimated to be 2534 km², which represents 37% of the total Gulf of Mexico mangrove cover (Table 2). Mangroves in the United States are most abundant in southern and central portions of the state of Florida (Table 2) (FDEP, 2016). Freeze-stunted mangrove stands are present in parts of Texas, Louisiana, and north Florida. The total mangrove coverages in Texas and Louisiana are comparatively small (Table 2). Isolated black mangrove individuals can occasionally be found on the barrier islands off the coast of Mississippi. However, the climatic conditions in the inland and more northern coastal wetlands of north Florida, Alabama, Mississippi, Louisiana, and Texas have historically (i.e., in recent decades and centuries) been too cold (i.e., freeze events have been too frequent and extreme) to enable mangrove establishment and dominance.

As mentioned previously, mangrove species richness in the Gulf of Mexico and the rest of the Atlantic East Pacific region is lower than in the Indo West Pacific region (Duke et al., 1998) (Fig. 3). There are three mangrove tree species that are particularly common along the Gulf of Mexico coast (Fig. 4): *Avicennia germinans* (L.) L. (black mangrove), *Rhizophora mangle* L. (red mangrove), and *Laguncularia racemosa* (L.) C.F. Gaertn. (white mangrove). Of these species, *A. germinans* is the most tolerant of cold temperatures and hypersaline conditions (McKee et al., 2004; Ross et al., 2009; Lovelock et al., 2016). Thus, *A. germinans* is the species that is most abundant near the northern limit of mangrove forests in Texas, Louisiana, and Florida and in the hypersaline conditions prevalent in the estuaries near the Mexico-United States border.
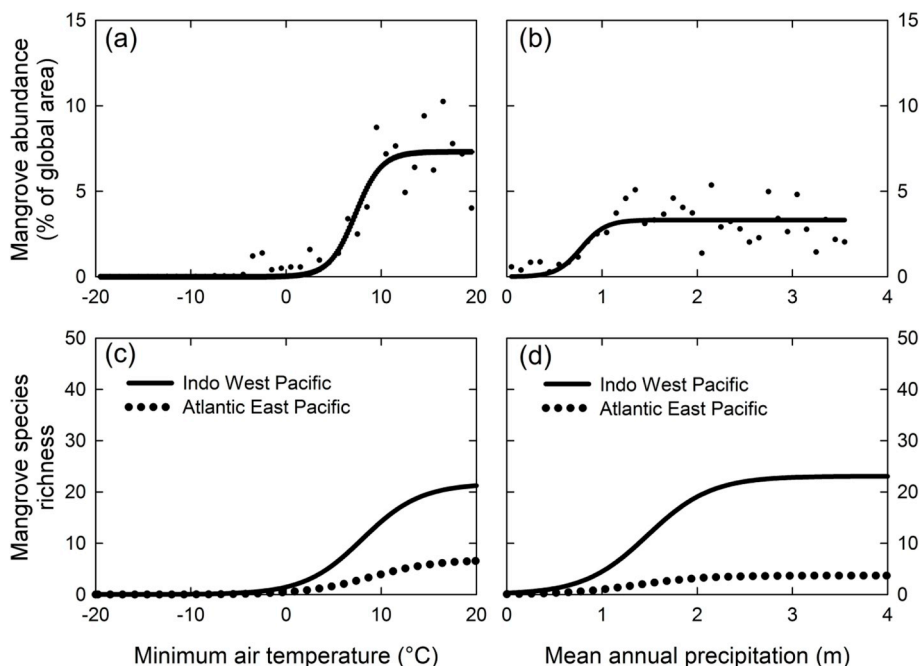

Fig. 3. Climatic factors control mangrove abundance and diversity. The relationships between: (a) minimum air temperature and global mangrove abundance; (b) mean annual precipitation and global mangrove abundance; (c) minimum air temperature and mangrove species richness, within the two major mangrove biogeographic zones; and (d) mean annual precipitation and mangrove species richness within the two major mangrove biogeographic zones. The two biogeographic zones are shown in Fig. 1. Figures adapted from Osland et al. (2017b).
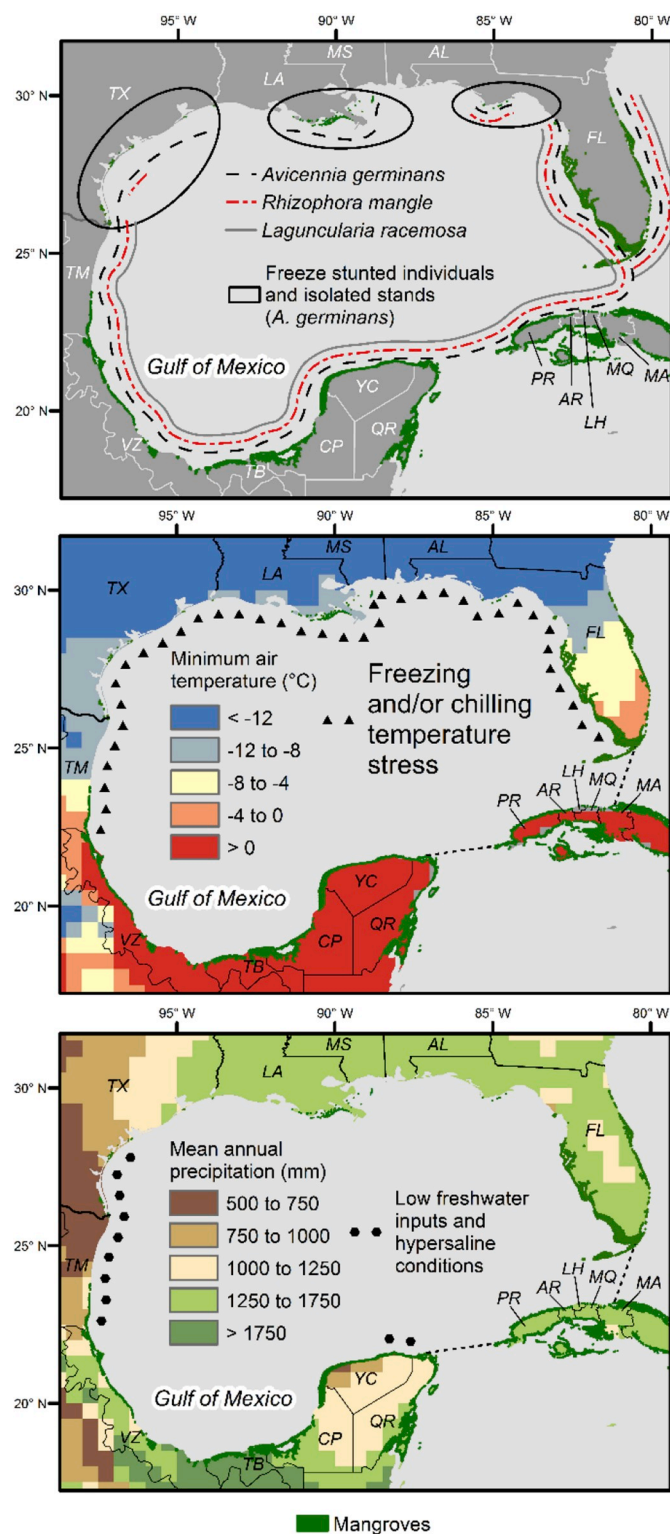
Fig. 4. Temperature and precipitation regimes greatly influence the distribution, structure, and function of mangroves forests along the Gulf of Mexico. Maps of: (upper) the distribution of mangrove forests and mangrove species' poleward limits along the Gulf of Mexico coast; (middle) minimum air temperature and areas where mangroves are vulnerable to freezing and/or chilling stress; and (bottom) mean annual precipitation and areas where mangroves are vulnerable to low freshwater inputs and hypersaline conditions. Mangrove distribution data are from: (1) Mexico: CONABIO (2016); (2) Cuba: Giri et al. (2011); (3) south and central Florida: FDEP (2016); (4) northwestern Florida: C. Snyder (Apalachicola NERR, personal communication); (5) Louisiana: R. Day (USGS, personal communication); (6) Texas: Sherrod and McMillan (1981) and Armitage et al. (2015). Two letter state abbreviations are described in Table 2.
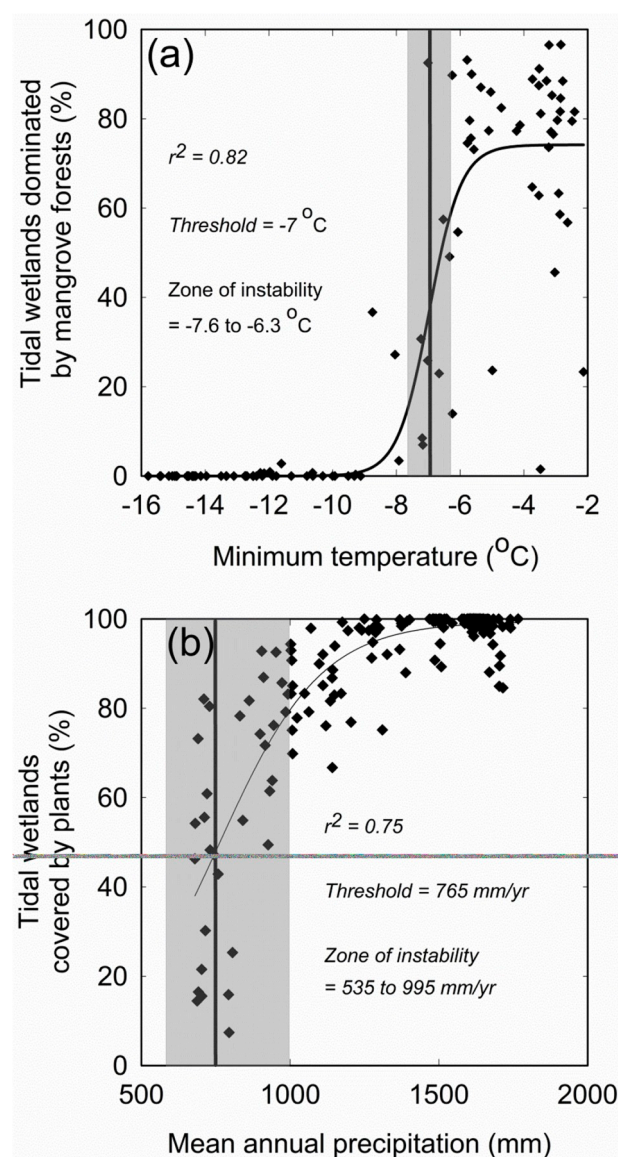

Fig. 5. For tidal saline wetlands along the Gulf of Mexico, the relationships between: (a) minimum air temperature and mangrove forest dominance in tidal saline wetlands; and (b) mean annual precipitation and plant coverage. Mangrove forest dominance (a) and plant coverage (b) were determined using remotely-sensed data. Figures adapted from Osland et al. (2013; 2014b; 2016).

The ecophysiological differences among species are reflected by the northern range limits of *A. germinans, R. mangle,* and *L. racemosa* along the northwestern (i.e., Texas and Louisiana) and northeastern (i.e., Florida) coasts of the United States (Fig. 4).

In addition to the effects on mangrove distribution and diversity, air temperature and precipitation regimes also affect the structure and function of mangrove forests in the Gulf of Mexico (Lovelock et al., 2016; Osland et al., 2016; Feher et al., 2017; Gabler et al., 2017). Mangroves in the colder northern portions of the Gulf of Mexico are often multi-stemmed and shrubby compared to their often single-stemmed tropical counterparts (Pool et al., 1977; Perry and Mendelssohn, 2009; Osland et al., 2014a; Yando et al., 2016; Guo et al., 2017). Similarly, mangrove forests in the hypersaline and drier portions of the Gulf of Mexico are typically shorter (< 3 m) than their taller counterparts (> 10 m) in wetter and less saline habitats (Lot-Helgueras et al., 1975; Lugo and Patterson-Zucca, 1977; Castañeda-Moya et al., 2006; Méndez-Alonzo et al., 2008).

Table 2
Mangrove coverage estimates for countries and states along the Gulf of Mexico coast including their estimated contributions to regional and global total mangrove coverage. Sources include: [a]Hamilton & Casey (2016); [b]Giri & Long (2016); [c]Armitage et al. (2015); [d]FDEP (2016); [e]Menéndez Carrera (2013); [f]CONABIO (2016); [g]Troche-Souza et al. (2016).

Country	State/Province	Mangrove cover (km²)	% of regional total	% of global total [a]
United States	Texas (TX)	34[b,c]	0.49	0.04
	Louisiana (LA)	15[b]	0.22	0.02
	Mississippi (MS)	0	0.00	0.00
	Alabama (AL)	0	0.00	0.00
	Florida (FL)	2485[d]	36.18	3.05
	United States total	**2534**	**36.89**	**3.11**
Cuba	Pinar del Río (PR)	403[e]	5.87	0.49
	Artemisa (AR)	49[e]	0.71	0.06
	La Habana (LH)	1[e]	0.01	0.00
	Mayabeque (MQ)	1[e]	0.01	0.00
	Matanzas (MA)	19[e]	0.28	0.02
	Cuba total	**473**	**6.88**	**0.58**
Mexico	Quintana Roo (QR)	72[f]	1.05	0.09
	Yucatán (YC)	932[g]	13.56	1.14
	Campeche (CP)	1989[g]	28.94	2.44
	Tabasco (TB)	454[g]	6.61	0.56
	Veracruz (VZ)	383[g]	5.58	0.47
	Tamaulipas (TM)	33[g]	0.48	0.04
	Mexico total	**3863**	**56.23**	**4.74**
Total		**6870**	**100.00**	**8.43**

3. Warming temperatures

Along the northern Gulf of Mexico coast, future changes in the intensity, duration, and frequency of winter air temperature extremes are expected to enable mangrove forests to expand northward at the expense of salt marshes (Ross et al., 2009; Day et al., 2013; Osland et al., 2013; Cavanaugh et al., 2014). In the past, the distribution of mangrove forests in North America has expanded and contracted in response to fluctuating temperature regimes (Sherrod and McMillan, 1985; Woodroffe and Grindrod, 1991; Sandoval-Castro et al., 2012, 2014; Saintilan et al., 2014; Kennedy et al., 2016, 2017; Osland et al., 2017a). During warmer periods, mangrove distribution in the northern hemisphere has expanded northward, and during colder periods, mangrove distribution has contracted southward (Fig. 6 and Fig. 7). Fossil records from warmer climates prior to the Pleistocene indicate that mangroves were once present in Tennessee and northern portions of Texas, Louisiana, Mississippi, Alabama, and Georgia (i.e., north of their current distribution) (Fig. 6) (Sherrod and McMillan, 1985; Westgate and Gee, 1990; Gee, 2001). A recent analysis of pollen records from Arctic Siberia indicates that mangrove were present there during the early Eocene (Suan et al., 2017). In contrast, fossil records from the Pleistocene indicate that the northern range limit of mangroves had contracted to more equatorial locations in the Caribbean (i.e., near Nicaragua and Trinidad) (Fig. 6) (Sherrod and McMillan, 1985). During the last glacial maximum, mangroves and many other tropical species were restricted to locations south of their current distribution. However, once the last glacial maximum ended approximately 19,000 years ago (Clark et al., 2009), mangroves began to expand poleward until reaching their current distribution (Sandoval-Castro et al., 2012, 2014; Kennedy et al., 2016, 2017).

Ecologists in the Gulf of Mexico region have long been fascinated by freeze events because of their ability to induce mortality, transform ecosystems, and define the northern range limits of many tropical and subtropical species (Olmsted et al., 1993; Ross et al., 2009). Many of the freeze events that lead to mangrove forest mortality also damage or kill other organisms (e.g., fish, manatee, sea turtles, reptiles, citrus) (Boucek et al., 2016; Osland et al., 2017a). Hence, a review of freeze events that have killed other organisms can provide a historical perspective regarding events that have likely led to mangrove mortality. For instance, Martin and McEachron (1996) provide a review of known freeze events that have affected marine organisms (e.g., fish and sea turtles) in Texas for the 19th and 20th centuries. For south Florida, Storey and Gudger (1936) provide a synopsis of notable freeze events that affected fishes between 1886 and 1934. Attaway (1997) provides a historical analysis of freeze events that caused citrus damage in Florida, Georgia, and South Carolina dating back to the late 17th century. Rogers and Rohli (1991) provide a description of citrus-damaging freeze events in Florida between 1880 and 1990. The northern limits of certain citrus hybrids in the southeastern United States are near the northern limit of mangrove forests (Stevens et al., 2006; Osland et al., 2017a). Hence, these citrus-focused descriptions are particularly useful given their century-scale temporal span.

Using air temperature records dating back to 1893, Osland et al. (2017a) hindcasted century-scale patterns of mangrove expansion and contraction in Louisiana (Fig. 7). Similar patterns of rapid contraction followed by progressive expansion are expected to have occurred in Texas and north Florida (i.e., mangrove mortality and habitat loss following extreme freeze events followed by habitat gain and northward expansion in between major freeze events). In a seminal early communication on mangrove ecology in south Florida, Davis (1940) briefly describes the effects of freeze events on mangroves between 1894 and 1936. For Cedar Key (Florida), Lugo and Patterson-Zucca (1977) provide descriptions of freeze events that occurred between 1914 and 1977 and also present an investigation of mangrove damage and mortality in the area following a 1977 freeze event. In the 1980s, multiple extreme freeze events caused substantial mortality and damage to mangroves across the northern Gulf of Mexico, including in Texas (Sherrod and McMillan, 1985; Lonard and Judd, 1991; Everitt et al., 1996), Louisiana (Perry and Mendelssohn, 2009; Giri et al., 2011; Osland et al., 2017a), and Florida (Olmsted et al., 1993; Stevens et al., 2006). A freeze event that occurred in December 1989 was the last (i.e., most recent) major freeze event to have severely affected mangroves in the region. Despite widespread mortality of mangrove trees in Louisiana during the 1989 freeze, Karen McKee (personal communication) noted that a very large number of mangrove propagules remained viable on the soil surface and available for post-dieback regeneration.

Since 1989, there has not been a region-wide freeze event along the Gulf of Mexico coast that has been comparable, in terms of the extent of mangrove mortality and habitat loss, to the multiple biologically-significant freeze events that occurred in the 1980s. Thus, mangroves have been progressively expanding, since 1989, in parts of Texas, Louisiana, and Florida (Giri et al., 2011; Montagna et al., 2011; Cavanaugh et al., 2014; Armitage et al., 2015; Giri and Long, 2016; Rodriguez et al., 2016; Osland et al., 2017a). Key areas of expansion under current monitoring and scientific research include the freeze-sensitive mangrove-marsh ecotones near Port Aransas (Texas), Galveston (Texas), Port Fourchon (Louisiana), Horn and Cat Islands (Mississippi), St. Joseph Bay (Florida), Apalachicola (Florida), and Cedar Key (Florida) (Table 3). Although there has not been a major freeze event since 1989, there have been several less severe freezing and chilling events that have caused a small amount of local mangrove damage and mortality. These events did not result in major habitat losses. However, they have provided valuable opportunities to advance our understanding of mangrove responses to freezing and chilling events (Ross et al., 2009; Pickens and Hester, 2011; Cavanaugh et al., 2014, 2015; Osland et al., 2015, 2017a; Zhang et al., 2016; Cavanaugh et al., 2018). Opportunistic
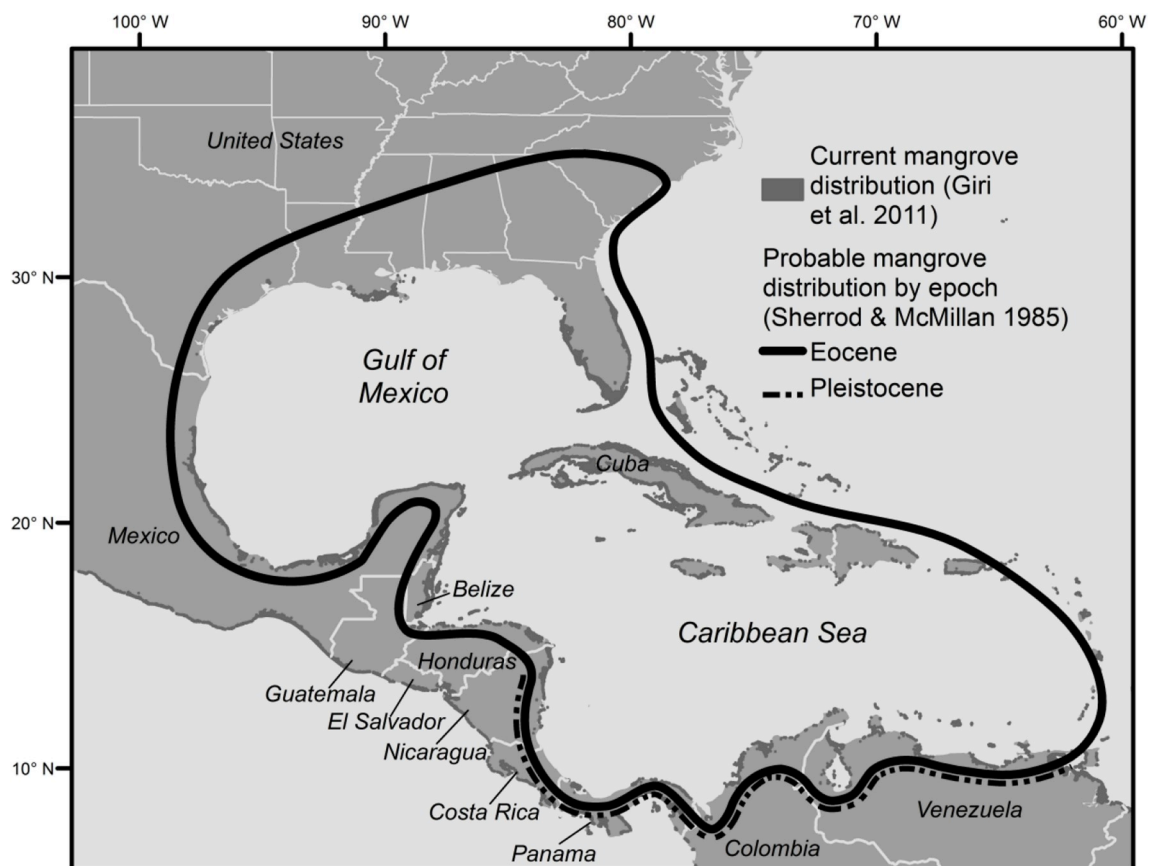
Fig. 6. In response to temperature fluctuations, mangrove distribution has expanded during warmer periods and contracted during colder periods. This map illustrates the current mangrove distribution (Giri et al., 2011) and the expected mangrove distribution during the Eocene and Pleistocene epochs (adapted from Sherrod and McMillan, 1985).
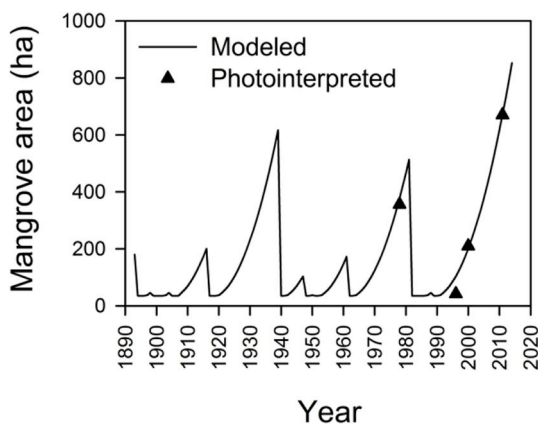

Fig. 7. Modeled and photointerpreted cycles of freeze-controlled mangrove expansion and contraction near Port Fourchon, Louisiana between 1893 and 2014. In this location and other areas of the northern Gulf of Mexico, mangrove forest coverage expands and contracts in the absence or presence of winter temperature extremes that lead to mangrove mortality. Figure from Osland et al. (2017a).

studies conducted immediately following these events identified ecologically-relevant microclimatic gradients and showed that mangrove resistance and resilience is species and life-stage dependent (Lugo and Patterson-Zucca, 1977; Pickens and Hester, 2011; D'Odorico et al., 2013; Pickens et al., 2018). For example, *A. germinans* is more freeze-tolerant (i.e., resistant) than *R. mangle* or *L. racemosa*, and *A. germinans* and *L. racemosa* are more resilient to freeze damage than *R. mangle* due to their ability to vigorously resprout from regenerative buds (Olmsted

et al., 1993; Ross et al., 2009). Post-freeze observations have also shown that *A. germinans* seedlings and taller trees are more freeze-resistant than juvenile trees, which may be indicative of positive feedbacks that could affect the rate of mangrove expansion (Osland et al., 2015). However, these positive feedbacks could be modulated by biotic interactions that alter seedling dynamics (Devaney et al., 2017; Langston et al., 2017). Another opportunistic study was conducted along the Shark River Estuary of Everglades National Park, where Danielson et al. (2017) showed that chilling temperatures defoliated riverine mangrove forests but caused limited mangrove mortality, and litterfall production levels reached seasonal mean values after one month.

Latitudinal data and experiments have shown that freeze-tolerance is highest near range limit edges (Markley et al., 1982; Madrid et al., 2014; Cook-Patton et al., 2015). Long-term observations and data from south Florida have been particularly useful for quantifying the species-specific effects of chilling events (Ross et al., 2009; Zhang et al., 2016). As the most freeze-tolerant species in the region, *A. germinans* is the species with the most northerly distribution and the species that is expected to first become established in locations beyond the current mangrove distribution. The other two common mangrove species in the region (i.e., *L. racemosa* and *R. mangle*) are more freeze sensitive than *A. germinans* (Olmsted et al., 1993; Ross et al., 2009; Day et al., 2013; Cavanaugh et al., 2015; Cook-Patton et al., 2015; Lovelock et al., 2016). Hence, these two species are only expected to appear in new areas after *A. germinans* has become established. However, if temperatures warm rapidly and freeze events begin to play a weakened role in setting range limits in the region, biotic interactions and species' dispersal capacity and recruitment traits may play an increasingly critical role and affect the sequence and extent of species migration and establishment. Due to the presence of land-ocean temperature gradients (i.e., colder air near

Table 3
Focal areas for scientific research on freeze-sensitive mangrove-marsh ecotones along the northern Gulf of Mexico coast. Mangroves in each of these areas have been expanding since the last major freeze-inducing mortality event occurred in 1989. Most of these studies focus on plant physiology or plant-plant interactions. The following symbols are used to denote studies that investigate the effects of mangrove expansion on: (A) = avian communities; (NI) = nekton communities or plant-invertebrate interactions; (PS) plant-soil interactions; (M) microclimate; and (W) plant water use.

Location	Scientific investigations
Port Aransas, Texas	McMillan, 1971; Sherrod and McMillan, 1981; Markley et al., 1982; Norman et al., 1984; Sherrod and McMillan, 1985; McMillan, 1986; McMillan and Sherrod, 1986; Sherrod et al., 1986; Montagna et al., 2011; Chavez-Ramirez and Wehtje, 2012 (A); Comeaux et al., 2012 (PS); Bianchi et al., 2013 (PS); Guo et al., 2013; Armitage et al., 2015; Yando et al., 2016 (PS); Diskin and Smee, 2017 (NI); Guo et al., 2017 (A, PS, M); Smee et al., 2017 (NI); Weaver and Armitage, 2018
Galveston, Texas	Guo et al., 2013; Madrid et al., 2014
Port Fourchon, Louisiana	Patterson and Mendelssohn, 1991; Patterson et al., 1993; Patterson et al., 1997; Caudill, 2005 (NI); Perry and Mendelssohn, 2009 (PS); Michot et al., 2010; Alleman and Hester, 2011a, b; Giri et al., 2011; Pickens and Hester, 2011; Henry and Twilley, 2013 (PS); Krauss et al., 2014a (W); Osland et al., 2014a; Osland et al., 2015; Yando et al., 2016 (PS); Osland et al., 2017a; Yando et al., 2018; Pickens et al., 2018
Horn Island, Mississippi	Scheffel et al., 2013; Scheffel et al., 2017 (NI)
St. Joseph Bay and Apalachicola, Florida	R. Hughes and C. Snyder, personal communication
Cedar Key, Florida	Lugo and Patterson-Zucca, 1977; Stevens et al., 2006; Yando et al., 2016 (PS); Langston et al., 2017 (NI); Yando et al., 2018

land and warmer air near the ocean), mangrove expansion and dominance is expected to occur first on barrier islands and wetlands that are close to warm gulf waters (Osland et al., 2017a). These areas are expected to serve as hot spots of dispersal and mangrove expansion into more inland wetlands.

Climate projections for the end of the 21st century indicate that there will be a decrease in the intensity, frequency, and duration of winter air temperature extremes (i.e., freeze events) in the Gulf of Mexico region and globally (IPCC, 2013; Parker and Abatzoglou, 2016; USGCRP, 2017). In response to warmer winter air temperatures, mangroves are expected to migrate northward and replace salt marshes (Day et al., 2013; Osland et al., 2013; Cavanaugh et al., 2015; Gabler et al., 2017). Historical temperature, mangrove presence, and mangrove abundance data have been used to identify ecological thresholds and model future mangrove presence and abundance across the region. Those analyses identify a minimum temperature-based threshold zone for mangrove dominance in the region between -6.3 and $-7.6\,°C$ (Osland et al., 2013, 2016). Whereas mangrove mortality and habitat loss are expected within and below this threshold zone, mangrove dominance is expected in areas with temperatures warmer than this threshold zone. The presence of an ecological threshold indicates that small changes in air temperature regimes can trigger large landscape-scale ecological changes as mangrove forests expand and replace salt marshes. This marsh-to-forest transition would constitute an ecological regime shift (sensu Scheffer et al., 2001; Scheffer and Carpenter, 2003) and would impact certain ecosystem goods and services. In addition to affecting fish and wildlife habitat (Caudill, 2005; Chavez-Ramirez and Wehtje, 2012; Diskin and Smee, 2017; Guo et al., 2017; Scheffel et al., 2017; Smee et al., 2017), mangrove expansion into salt marsh could affect carbon storage and cycling (Perry and Mendelssohn, 2009; Comeaux et al., 2012; Bianchi et al., 2013; Henry and Twilley, 2013; Lewis et al., 2014; Doughty et al., 2016; Kelleway et al., 2016; Yando et al., 2016; Simpson et al., 2017), elevation change in response to sea-level rise, wave attenuation, microclimate, nutrient processing, support of coastal food webs, and coastline erosion rates (Guo et al., 2017; Kelleway et al., 2017). The rate of mangrove expansion will be mediated by interactions between many factors including salinity, drought, life stage, dispersal rates, nutrient availability, and biotic interactions (McKee and Rooth, 2008; Alleman and Hester, 2011a, b; Pickens and Hester, 2011; Peterson and Bell, 2012; Guo et al., 2013; Simpson et al., 2013; Krauss et al., 2014a; Osland et al., 2015; Coldren et al., 2016; Langston et al., 2017; Simpson et al., 2017). Future projections indicate that salt marshes in Texas, Louisiana, and certain parts of north Florida are particularly vulnerable to mangrove expansion in response to warmer temperatures (Osland et al., 2013). These are the coastal areas where scientists and managers should be planning for and anticipating the positive and negative effects of mangrove expansion and salt marsh

loss including the potential implications for ecosystem goods and services.

4. Precipitation and hydrologic variability

Climate and land use change are expected to greatly alter hydrologic regimes and the availability of freshwater resources across the globe (Vörösmarty et al., 2000; Jackson et al., 2001). Mangrove forests in arid and semi-arid climates are particularly vulnerable to changes in rainfall and freshwater availability (Noy-Meir, 1973; Maestre et al., 2012; Reed et al., 2012; Lovelock et al., 2017). Along arid and semi-arid coasts, the reduction of freshwater inputs can lead to hypersaline conditions that hinder mangrove establishment, growth, and/or survival (Lovelock et al., 2016). Thus, fluctuations in freshwater availability can lead to fluctuations in mangrove coverage and physiological performance (Diop et al., 1997; Eslami-Andargoli et al., 2009; Asbridge et al., 2015). Mangrove forests in the following regions are particularly sensitive to changes in freshwater availability: western North America, western Gulf of Mexico, western South America, northwestern Africa, western central Africa, eastern central Africa, the Middle East, and western Australia (Fig. 1). Using global mangrove and precipitation data, Osland et al. (2017b) characterized positive sigmoidal relationships between precipitation and mangrove presence and species richness for these freshwater-controlled mangrove range limits (Fig. 3).

In the coming century, changing precipitation, hydrologic, and estuarine salinity regimes are expected to alter certain mangrove forests along the Gulf of Mexico coast (Montagna et al., 2007, 2011; Osland et al., 2014b, 2017b; Gabler et al., 2017). The Gulf of Mexico spans ecologically-relevant precipitation gradients that directly and indirectly govern the structure and function of mangrove forests (Méndez-Alonzo et al., 2008). Most estuaries in the region are located in wet climates with sufficient freshwater inputs such that salinity concentrations are typically highest near the ocean and lowest in the interior of the estuary close to riverine inputs (e.g., the Grijalva-Usumancinta Delta). However, in estuaries located in arid and semi-arid climates with minimal freshwater inputs and limited oceanic exchange, oceanic salts can accumulate in estuarine waters and coastal wetland soils, which can produce hypersaline conditions that are unsuitable for mangrove establishment and survival (Zedler, 1982; Semeniuk, 2013; Lovelock et al., 2017). In such estuaries, mangrove coverage and growth is highest close to the mouth of tidal inlets where salinities are lower and modulated by tidal exchange. For example, the Laguna Madre estuarine system of Texas and Tamaulipas, near the United States-Mexico border, is a hypersaline reverse estuary with salinities that are typically lowest near the ocean and highest towards the interior of the estuary (Tunnell and Judd, 2002). The Ría Lagartos estuary, parallel to the northern coast of the Yucatán Peninsula in Mexico, is also a hypersaline reverse

estuary due to very low groundwater flux in the three easternmost basins (Las Coloradas, El Cuyo, and Flamingos) and to their constrained connection with the westernmost seaward-connected Ría Lagartos basin (Herrera-Silveira et al., 1998; Smith et al., 1999); here, mangrove distribution and productivity are controlled by interannual variation in precipitation and groundwater flow to the coastal zone (Perry et al., 2009; Aragón-Moreno et al., 2012; Pérez-Ceballos et al., 2012). The hypersaline conditions in both of these estuaries limit mangrove coverage in the interior of the estuary and result in extensive unvegetated hypersaline tidal flats (Withers, 2002; Osland et al., 2014b; Gabler et al., 2017).

Although ecologists have long known that precipitation and salinity regimes govern the global distribution, abundance, and species richness of mangrove forests (Lugo and Snedaker, 1974; Cintrón et al., 1978; Saenger, 2002; Spalding et al., 2010), data constraints, both ecological and climatic, have historically hindered the quantification of precipitation-ecological linkages for coastal wetlands. Recent improvements in data quality and availability have improved our understanding of climatic controls on mangrove forests and other tidal saline wetland ecosystems. In an early and insightful communication regarding the influence of precipitation and salinity controls on mangrove forests along Mexico's gulf coast, Lot-Helgueras et al. (1975) described the relationship between precipitation regimes and the above-ground structure and composition of mangrove forests (see also: Lugo and Patterson-Zucca, 1977). Méndez-Alonzo et al. (2008) refined those analyses using field-collected data to quantify the relationship between precipitation and mangrove tree height and maximum diameter. Feher et al. (2017) presented hypotheses regarding precipitation and temperature controls of mangrove biomass, height, productivity, decomposition, and soil carbon density and accumulation, and used literature-derived data to quantify precipitation-based thresholds and non-linear relationships between precipitation and mangrove above-ground biomass and canopy height. However, those analyses highlight the need for additional productivity, decomposition, and soil carbon density and accumulation data that span ecologically-relevant precipitation gradients (see also Osland et al., 2018).

Using precipitation and remotely-sensed wetland habitat data, Deegan et al. (1986), Longley (1994, 1995), Montagna et al. (2007, 2011), and Osland et al. (2014b; 2017a) have shown that there is a positive sigmoidal relationship between precipitation and plant coverage in Gulf of Mexico coastal wetlands (Fig. 5b). A similar relationship has also been identified in Australian coastal wetlands by Bucher and Saenger (1994). Using field-based data collected in ten estuaries across the northern Gulf of Mexico, Gabler et al. (2017) characterized precipitation controls on tidal saline wetland vegetation height, above-ground biomass, and plant functional group dominance (i.e., mangrove, graminoid, succulents, and unvegetated). The results of Osland et al. (2014b) and Gabler et al. (2017) show that the positive relationship between coastal wetland plant coverage and precipitation along the northern Gulf of Mexico coast is nonlinear and sigmoidal. Osland et al. (2014b) identified a precipitation-based threshold zone for coastal wetland plant coverage that occurs when mean annual precipitation is approximately 995 mm. Mechanistically, this precipitation threshold is expected to correspond to surface and porewater salinity levels (e.g., > 50 ppt) that hinder plant performance and influence species diversity and zonation (Cintrón et al., 1978; Castañeda-Moya et al., 2006). Those results indicate that for coastal wetlands that are above this threshold, small changes in precipitation are not expected to result in long-term changes in plant coverage. However, for coastal wetlands that are below this threshold, small changes in precipitation can trigger large changes in plant coverage. Increases or decreases in precipitation would, respectively, increase or decrease plant coverage and alter plant community composition (Osland et al., 2014b; Gabler et al., 2017). Indeed, long-term data demonstrate that coastal wetland plant community composition and coverage in arid and semi-arid climates oscillate in response to variability in precipitation and freshwater

availability (Diop et al., 1997; Dunton et al., 2001; Forbes and Dunton, 2006; Eslami-Andargoli et al., 2009). A striking, recent example comes from northern and western Australia, where a sudden and severe dieback of mangrove forests in 2015–2016 apparently was caused by the interaction of low precipitation, high temperatures, and low sea level (Duke et al., 2017; Lovelock et al., 2017).

In coastal wetlands, marsh and mangrove plants are considered foundation species, which are species that create habitat, modulate ecosystem functions, and support entire ecological communities (sensu Dayton, 1972; Ellison et al., 2005). Due to the critical role of plants in coastal ecosystems, changes in plant coverage and composition have important implications for the provision of coastal wetland ecosystem goods and services. Although the effects of precipitation change are expected to be greatest in estuaries along dry coasts (i.e., under current climate regions, in Texas and Tamaulipas near the Texas-Mexico border, and the northern coast of the Yucatán peninsula), changing precipitation regimes can also affect wetlands in high-precipitation areas. For example, in a mangrove-marsh ecotone in Louisiana, extreme drought events have resulted in acute dieback of *Spartina alterniflora* marshes (McKee et al., 2004), which can alter biotic interactions (Silliman et al., 2005) and result in periods of increased mangrove recruitment, growth, and expansion (McKee and Rooth, 2008; Krauss et al., 2014a).

In addition to climate change, coastal development and urban growth can also negatively affect mangrove forest hydrology via changes to the amount, quality, quantity, and timing of freshwater and sediment delivery to estuaries and mangrove forests (Alber, 2002; U.S. Army Corps of Engineers and South Florida Water Management District, 2012; Montagna et al., 2013; Michot et al., 2015; Howard et al., 2017). Like all estuarine ecosystems, mangrove forest structure, function, and stability are greatly influenced by hydrologic, salinity, and sediment delivery regimes, which are abiotic regimes that are often modulated by estuarine freshwater inputs. Such changes are compounded by the effects of sea-level rise which include saltwater intrusion and increased inundation. There is a pressing need across the entire Gulf of Mexico coast (i.e., United States, Mexico, and Cuba) to better anticipate and prepare for the effects of altered freshwater inputs on mangrove forests. Due to increasing human water demands and climate change-induced alterations to the hydrological cycle, we expect that scientists and environmental managers will be increasingly urged to define the minimum freshwater inputs and hydrologic regimes that are needed to sustain mangrove ecosystems for future generations.

5. Sea-level rise

Since inundation and salinity regimes are two of the most important abiotic drivers of mangrove ecosystem structure and function, accelerated sea-level rise is expected to have a large effect on mangrove forests (Ellison and Stoddart, 1991; Parkinson et al., 1994; Williams et al., 1999; Krauss et al., 2014b; Alongi, 2015; Doyle et al., 2015; Lovelock et al., 2015; Ward et al., 2016; Woodroffe et al., 2016). Small changes in inundation and/or salinity regime can trigger abrupt and dramatic ecological changes (i.e., ecological regime shifts) (Ball, 1988; Woodroffe, 1990; Mendelssohn and Morris, 2000; Lovelock et al., 2010, 2016; Friess et al., 2011). For example, near the mangrove-open water ecotone (i.e., lower intertidal elevations and near critical thresholds), small increases in inundation can result in the submergence and loss of mangrove forests. Conversely, near mangrove ecotones at higher intertidal elevations and/or near the saltwater-freshwater interface, small changes in inundation and/or salinity can result in the landward migration of mangrove forests at the expense of upslope or upriver ecosystems (Ross et al., 1994, 2000; Williams et al., 1999; Doyle et al., 2010; Krauss et al., 2011; López-Medellín et al., 2011; Enwright et al., 2016; Howard et al., 2017).

The Gulf of Mexico coast spans diverse geomorphic gradients (Ortiz Pérez, 2016) that modulate wetland responses to sea-level rise. Coastal
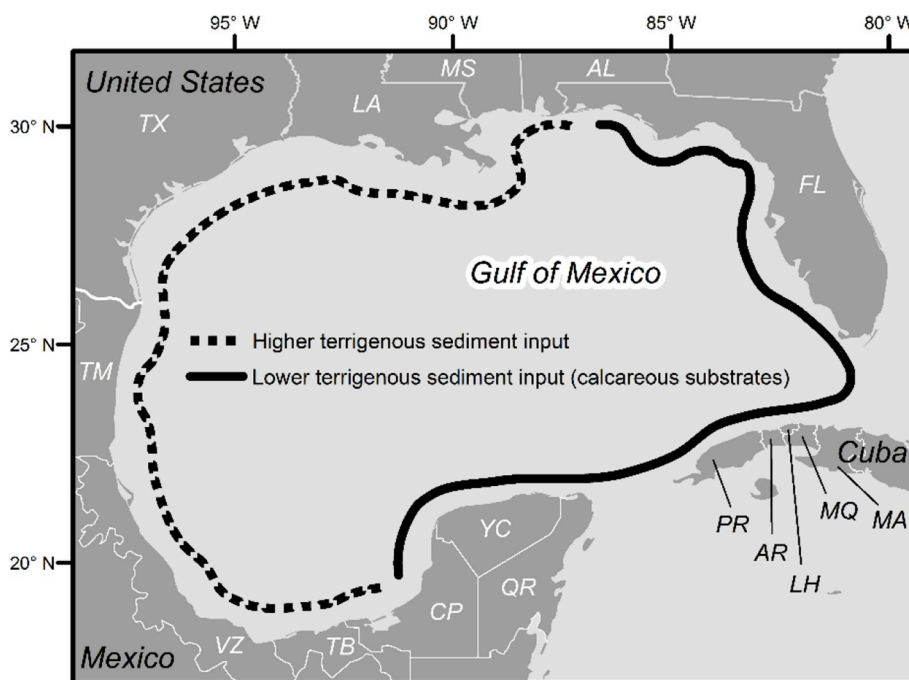
Fig. 8. Map showing coastal areas of the Gulf of Mexico with high and low terrigenous sediment inputs (adapted from: Balsam and Beeson, 2003; Ellwood et al., 2006). The productivity and structure of mangrove forests growing on calcareous substrates is often limited by phosphorus availability. Mangrove soil development and accretion in these karstic regions are often highly dependent upon biogenic processes and groundwater flow, because sediment inputs are low.

wetlands in the region are located in large sediment-dependent deltas (e.g., the Grijalva-Usumacinta delta) and also along karst-dominated and sediment-poor oligotrophic coasts (e.g., Celestun Lagoon) (Fig. 8). Along the southern and southwestern Gulf of Mexico coast, mangrove forests grow primarily on calcareous substrates with minimal terrigenous sediment inputs. However, mangrove forests and other coastal wetlands along the western, northeastern, and northern Gulf of Mexico coasts receive higher terrigenous sediment inputs (Fig. 8) (Balsam and Beeson, 2003; Hudson and Heitmuller, 2003; Reyes et al., 2004; Ellwood et al., 2006; Muñoz-Salinas and Castillo, 2015). Hence, mangrove forest responses to sea-level rise in the Gulf of Mexico region are diverse and greatly influenced by sediment inputs and local geomorphic settings.

Several recent communications provide valuable descriptions of the ecogeomorphic processes that govern mangrove forest responses to sea-level rise (McKee et al., 2007; McKee, 2011; Krauss et al., 2014b; Lovelock et al., 2015; Woodroffe et al., 2016). To persist during sea-level fluctuations, mangrove ecosystems must adjust their vertical and/or horizontal position in the landscape. Some mangroves can adjust vertically due to ecogeomorphic feedbacks between inundation, plant growth, and sedimentation (Morris et al., 2002; Kirwan and Murray, 2007; McKee et al., 2007; Friess et al., 2011; Krauss et al., 2014b). Within deltas and alluvial environments, mineral sediment accumulation rates play an important role and greatly influence surface elevation change in mangrove forests (Woodroffe, 1990; Lovelock et al., 2010, 2015; Woodroffe et al., 2016). However, in mangrove forests that receive small or no external sediment inputs (e.g., oceanic islands and carbonate-dominated coasts like those found in south Florida, the Yucatán Peninsula, and throughout the Caribbean), biotic contributions play an especially important role (Breithaupt et al., 2017). Mangrove ecosystem stability and vertical adjustment in the face of sea-level change are greatly influenced by plant productivity, peat development, and the accumulation of refractory mangrove roots and benthic mat materials (McKee et al., 2007; McKee, 2011; Krauss et al., 2014b). These biotic contributions have enabled some mangrove forests to adjust vertically to thousands of years of small-to-moderate sea-level rise. However, under higher rates of sea-level rise, submergence and local loss of certain mangrove forests has occurred in the past and is expected in the future (Woodroffe, 1990; McKee et al., 2007; Donoghue, 2011; Doyle et al., 2015; Lovelock et al., 2015). Within the Gulf of Mexico

region, the poster child for coastal wetland loss is the Mississippi River Delta Plain, where coastal wetland losses (primarily salt marsh) have been very large due to rates of relative sea-level rise that can exceed 2 cm/year (Jankowski et al., 2017).

In addition to vertical adjustments, mangrove forests can adjust to sea-level rise via horizontal movement across the landscape (i.e., landward migration, transgression, inland migration). Landward migration occurs via propagule dispersal, establishment, and mangrove forest growth in adjacent ecosystems (e.g., upslope or upriver grasslands, marshes, and forests). Coastal squeeze is a term that refers to the loss of intertidal habitat when a barrier prevents landward migration in response to sea-level rise (Torio and Chmura, 2013; Woodroffe et al., 2016). Coastal cities along the Gulf of Mexico are growing rapidly, which is increasing the amount of flood control infrastructure and decreasing the amount of land available for landward migration of mangrove forests and other coastal ecosystems. In low-lying sections of the Gulf of Mexico's highly urbanized estuaries (e.g., Tampa Bay and Charlotte Harbor in south Florida; Havana in Cuba; Ciudad del Carmen in Campeche, Mexico), the landward migration of certain mangrove forests will be prevented by levees and coastal development (Enwright et al., 2016; Borchert et al., 2018). To avoid coastal squeeze, there is an urgent need to identify migration corridors that will allow mangroves to migrate landward in response to sea-level rise. In the absence of natural or anthropogenic barriers, mangrove forests are expected to move landward into adjacent upslope and/or upriver ecosystems.

Elevations along much of the Gulf of Mexico coast are low enough that, at the regional scale, the amount of land available for landward migration of mangrove forests is very large (Ortiz Pérez and Méndez Linares, 1999; Doyle et al., 2010; Martínez et al., 2014; Enwright et al., 2016; Hernández-Montilla et al., 2016) (Fig. 9). For Mexico, Ortiz Pérez (2016) provides a valuable classification of the country's coasts according to geomorphologic controls and the change that has occurred due to erosion or sediment accumulation. Those analyses identify certain areas (e.g., parts of Tabasco and Campeche) where decreases in sediment input and high rates of subsidence have resulted in rapid rates of land loss. In addition to hot-spots of high subsidence, Tabasco and Campeche also have large areas of low-lying land that are vulnerable to rising sea levels (Fig. 9).

For the United States, Enwright et al. (2016) use tidal datum-wetland relationships to quantify the amount of land available for wetland
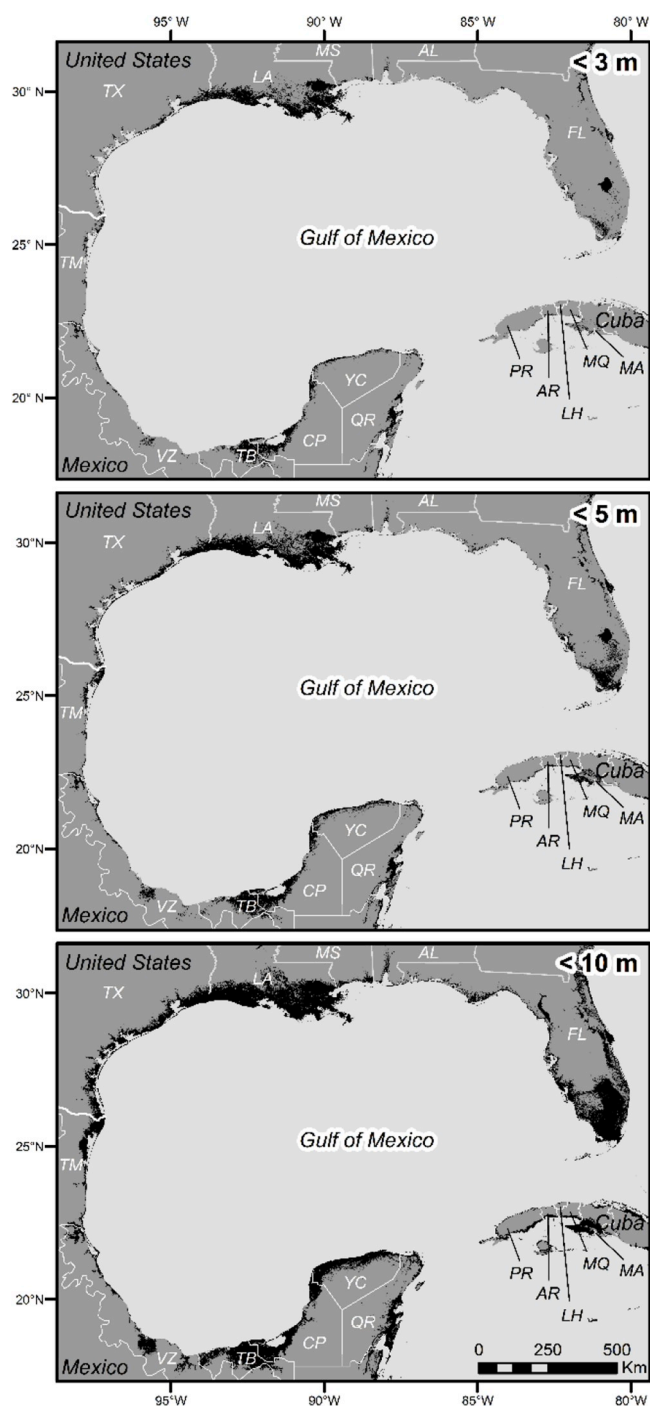
Fig. 9. Map of elevations below 3 m (top), 5 m (middle), and 10 m (bottom) along the Gulf of Mexico coast. Elevation data are from the SRTM (Shuttle Radar Topographic Mission) v4.1 global digital elevation model data at a resolution of 250 m (Reuter et al., 2007). These maps provide a coarse, initial identification of low-lying lands that are vulnerable to the combined effects of rising sea levels and elevated storm surge impacts associated with hurricanes.

migration under different sea-level rise and urbanization scenarios. For example, the Mississippi River Deltaic Plain of coastal Louisiana and the Everglades region of south Florida stand out as areas where the effects of sea-level rise will be especially large because of their low-lying topography (Fig. 9). High rates of subsidence and relative sea-level rise will intensify and hasten the effects of eustatic sea-level rise in certain areas (e.g., in Louisiana and east Texas). In the Mississippi River Deltaic Plain of coastal Louisiana, annual subsidence rates can exceed 1 cm/

year and the rate of coastal wetland loss has been rapid (i.e., ~4900 km^2 of coastal wetland loss since 1932) due partly to high rates of relative sea-level rise (Day et al., 2007; Blum and Roberts, 2009; Couvillion et al., 2011; Twilley et al., 2016). Mangrove forests in the Mississippi River Deltaic Plain are experiencing rates of relative sea-level rise that are higher than most other mangrove forests in the region. Currently, mangrove forests only cover a very small portion of the Mississippi River Delta. However, with changing winter air temperature regimes, mangrove forests in the delta are expected to expand at the expense of salt marsh, and the persistence of these mangrove forests will be dependent upon their ability to adjust and adapt to sea-level rise.

6. Tropical cyclone intensification

Tropical cyclones (i.e., hurricanes, typhoons) are major ecological disturbances that can have a tremendous impact on mangrove ecosystems (Smith III et al., 1994; Doyle et al., 1995; Menéndez Carrera, 2013; Ward et al., 2016) (Fig. 10). In the Indian Ocean, tropical cyclones affect non-equatorial mangrove forests (i.e., mangrove forests along the coasts of western Australia, southeastern Africa, Bay of Bengal, and western Arabian Sea). In the Pacific Ocean, tropical cyclones influence mangrove forests adjacent to Mexico, Central America, southeastern Asia, and eastern Australia. In the Atlantic Ocean, tropical cyclones affect mangrove forests adjacent to the Caribbean Sea, the Gulf of Mexico (Calderon-Aguilera et al., 2012; Farfán et al., 2014), and the Atlantic coast of North America. However, there are certain regions of the world where tropical cyclones are not present (Knapp et al., 2010), for example the Pacific and Atlantic coasts of South America, the Atlantic coast of Africa, and equatorial regions across the world (Fig. 10).

Due to climate change, tropical cyclone intensity is expected to rise in the coming century. The number of large tropical cyclones (i.e., category 4–5 on the Saffir-Simpson Hurricane Wind Scale) is expected to increase (Knutson et al., 2010, 2015; Sobel et al., 2016), and the impacts from increased cyclone intensity will be exacerbated by rising sea levels (Scavia et al., 2002). Since cyclones greatly influence the structure and function of mangrove forests (Conner et al., 1989; Smith III et al., 1994; Doyle et al., 1995; Doyle et al., 2002; Cahoon et al., 2003; Adame et al., 2013b), climate-change induced increases in cyclone intensity are expected to have a large impact on mangrove forests in certain regions of the world, particularly in the Gulf of Mexico (Fig. 10). The high winds, storm surge, saltwater intrusion, and extreme precipitation produced by cyclones can knock down entire forests, induce peat collapse, deposit thick sediment layers, provide valuable subsidies of limiting nutrients (e.g., phosphorus), lead to erosion, alter hydrologic connectivity, and thus transform forest plant communities (Roth, 1992; Smith III et al., 1994; Doyle et al., 1995; Chen and Twilley, 1999b; Baldwin et al., 2001; Cahoon et al., 2003; Krauss et al., 2005; Cahoon, 2006; Whelan et al., 2009; Castañeda-Moya et al., 2010; Rivera-Monroy et al., 2011; Barr et al., 2012; Adame et al., 2013b; Danielson et al., 2017).

Cyclone effects on mangrove forests are diverse, and most of our knowledge derives from opportunistic measurements conducted immediately following a cyclone event. In many regions of the world, including the Gulf of Mexico, there is a pressing need for continued improvements to our understanding of the long-term effects of cyclones on mangrove forest ecosystem structure and function. Conversely, there is also a need to improve our understanding of the ecosystem services provided by mangrove forests that relate to coastal protection. Mangrove forests can protect coastal communities from storms via the attenuation of wave and wind energy, enhanced sedimentation, and reduced erosion (Alongi, 2008; Costanza et al., 2008; Krauss et al., 2009; Gedan et al., 2011; Lee et al., 2014; Marois and Mitsch, 2015; Sutton-Grier et al., 2015).
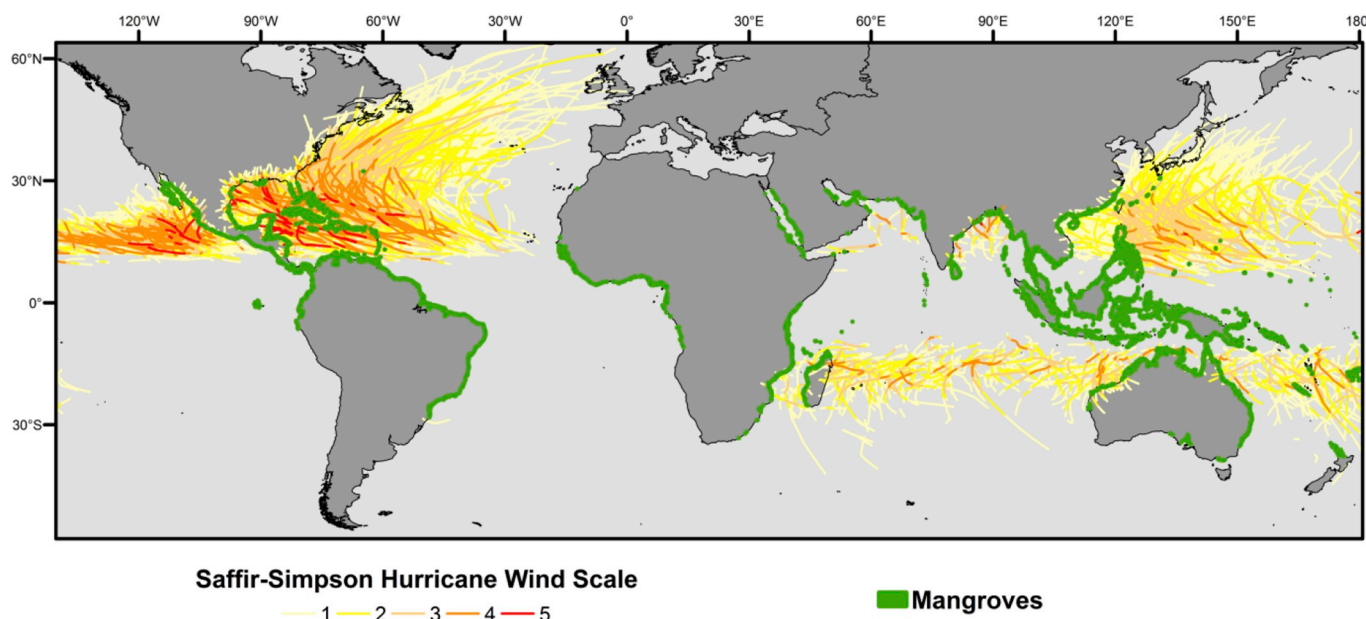
Fig. 10. Map of historical global tropical cyclone activity (Knapp et al., 2010) in relation to the distribution of mangrove forests (Giri et al., 2011).

7. Elevated atmospheric carbon dioxide

Atmospheric carbon dioxide concentrations have been increasing since the start of the industrial revolution and are expected to continue to increase in the coming century (IPCC, 2013). McKee and Rooth (2008), Krauss et al. (2008), McKee et al. (2012), Saintilan and Rogers (2015), Lovelock et al. (2016), and Reef et al. (2016) provide recent discussions of some of the known and expected effects of elevated atmospheric carbon dioxide on mangrove forests. Saintilan and Rogers (2015) hypothesize that elevated atmospheric carbon dioxide concentrations (i.e., a global driver) may modulate and enhance the effects of local abiotic drivers (e.g., changing inundation and/or salinity regimes) upon mangrove encroachment into adjacent ecosystems. Under certain abiotic conditions, elevated carbon dioxide concentrations are expected to increase mangrove productivity and water use efficiency, which could increase above- and below-ground biomass, alter biotic interactions, and increase mangrove extent and coverage (Ball and Munns, 1992; Farnsworth et al., 1996; Ball et al., 1997; McKee and Rooth, 2008; Cherry et al., 2009; Langley et al., 2009; McKee et al., 2012; Reef et al., 2015, 2016; Saintilan and Rogers, 2015; Lovelock et al., 2016). However, these effects are highly variable and dependent upon other factors, including nutrient availability, salinity regimes, and biotic interactions (Ball et al., 1997; McKee and Rooth, 2008; Reef et al., 2015, 2016; Lovelock et al., 2016). Near the poleward limit of mangroves and within a mangrove-marsh ecotone in Louisiana's Mississippi River Deltaic Plain, McKee and Rooth (2008) evaluated the multi-factorial effects of elevated carbon dioxide, nitrogen enrichment, and competition on interactions between a C_4 marsh species (*Spartina alterniflora*) and a C_3 mangrove species (*A. germinans*). Their results show that the ecological influence of elevated carbon dioxide in mangrove forests is context dependent and greatly influenced by many other factors (e.g., plant competition, life stage, nitrogen enrichment).

8. Nutrient availability

Nutrient availability greatly influences mangrove forest structure and function (Lugo and Snedaker, 1974; Feller, 1995; Chen and Twilley, 1999a; McKee et al., 2007; Krauss et al., 2008; Alongi, 2009; Medina et al., 2010; Reef et al., 2010; Twilley and Day, 2012; Rovai et al., 2018). Within a given wetland complex, nutrient limitation can vary greatly across environmental gradients due to differences in inundation, salinity, hydrologic connectivity, and sedimentation (Boto and Wellington, 1983; Feller et al., 2003; Lovelock et al., 2010). However, in general, mangroves growing on sediment-rich terrigenous substrates are expected to have a high potential for nitrogen limitation, and mangroves growing on calcareous carbonate-rich substrates are expected to have a high potential for phosphorus limitation (Ewe et al., 2006; Feller et al., 2007; Lovelock et al., 2007; Twilley and Rivera-Monroy, 2009).

Along the southern and southeastern Gulf of Mexico coast, phosphorus limitation is particularly common because mangrove forests have developed on calcareous substrates in the absence of large terrigenous sediment inputs (Fig. 8) (Feller, 1995; Koch and Snedaker, 1997; Chen and Twilley, 1999a; McKee et al., 2007; Medina et al., 2010; Adame et al., 2013b). Along the northern, northwestern, and southwestern Gulf of Mexico coast, nitrogen limitation is expected to play a more important role because mangrove forests in these areas receive phosphorus-rich terrigenous sediment inputs (Fig. 8). Nitrogen limitation in the terrigenous sediment-dominated mangrove forests of the Gulf of Mexico has not been widely studied. However, phosphorus limitation in carbonate-dominated mangrove forests is striking and has received much attention in the literature. In terms of aerial coverage, the karstic coastal reaches contain some of the largest and most significant mangrove forests in the Gulf of Mexico region (Fig. 4, Table 2). For example, the Yucatán Peninsula of Mexico (i.e., the states of Campeche, Yucatán, and Quintana Roo) (Bauer-Gottwein et al., 2011; Adame et al., 2013a, 2013b), the Cuban coast (Rejmánková et al., 1995; León and Parise, 2009), and the Everglades wetlands of south Florida (Noe et al., 2001; Richardson, 2008) all contain calcareous substrates (Fig. 8) where mangrove forests and the adjacent inland freshwater wetland ecosystems can be oligotrophic and highly sensitive to phosphorus inputs.

In karstic landscapes, the productivity and structure of mangrove forests and other estuarine ecosystems are often limited by phosphorus availability. In many estuaries, terrestrial and riverine inputs are typically the primary source of limiting nutrients, and the downstream and upstream limiting nutrients are typically nitrogen and phosphorus, respectively. In contrast, in the oligotrophic phosphorus-limited estuaries of karstic landscapes, the ocean can be the primary source of the limiting nutrient (phosphorus) (Fourqurean et al., 1992; Chen and Twilley, 1999a; Rudnick et al., 1999; Rivera-Monroy et al., 2011). Hence, karstic estuaries like the Everglades have been called "upside-down" estuaries

(Childers et al., 2006) because the limiting nutrient is typically phosphorus and the primary source of the limiting nutrient is the ocean rather than land.

In both the Yucatán and the Everglades, small increases in phosphorus availability have been found to cause comparatively large changes in mangrove forest structure and function (Koch, 1997; Chen and Twilley, 1999a; Rivera-Monroy et al., 2011; Adame et al., 2013b; Castañeda-Moya et al., 2013). The physiological constraints presented by oligotrophic conditions can produce scrub mangrove trees (e.g., trees with heights less than 1.5 m) (Lugo and Snedaker, 1974; Feller, 1995; Medina et al., 2010), and taller forests can develop in areas with higher phosphorus availability (Chen and Twilley, 1999a). Mangrove ecologists working in the Everglades have long been intrigued by the influence of nutrient availability on the striking spatial patterns of mangrove forest structure and function across the Everglades freshwater-to-ocean transition zone (Davis, 1940; Chen and Twilley, 1999a; Simard et al., 2006; Twilley and Rivera-Monroy, 2009; Castañeda-Moya et al., 2013). The Everglades contains some of the most widely studied oligotrophic mangrove forests in the world, in part due to research supported by the U.S. National Science Foundation-funded Florida Coastal Everglades Long-Term Ecological Research (LTER) Network (Rivera-Monroy et al., 2011). The freshwater-to-ocean transition zone in the Everglades spans a phosphorus availability gradient (i.e., higher phosphorus availability close to the ocean and lower phosphorus availability inland) (Boyer, 2006; Childers et al., 2006). In general, mangrove forest height, biomass, and productivity in this region are all highest in areas close to the ocean where phosphorus availability is greatest. Conversely, lower phosphorus concentrations on the freshwater side of the transition constrain mangrove growth (Chen and Twilley, 1999a; Davis et al., 2005; Rivera-Monroy et al., 2011; Castañeda-Moya et al., 2013). Phosphorus availability is also one of the most important abiotic controls on mangrove forest structure and function on the Yucatán Peninsula as shown by the positive relationships between soil phosphorus and mangrove litterfall (Adame et al., 2013b), above- and below-ground carbon stocks (Adame et al., 2013a), and root biomass and production (Adame et al., 2014). Given the tremendous ecological influence of phosphorus availability along the Yucatán, the Everglades, and other karstic coastal reaches of the southern Gulf of Mexico, future changes in phosphorus availability, due to sea-level rise, ground or surface water enrichment, hurricanes, hydrologic alterations, and other aspects of global change are expected to greatly influence the future structure, function, and stability of mangrove forests. Hence, predictions of the effects of global change (e.g., sea-level rise) in these areas should consider and account for the interactive effects of concomitant changes in nutrient availability.

9. Invasive non-native species

Invasive non-native species are a significant component of anthropogenic global change due to their tremendous impact upon the structure and function of terrestrial, aquatic, and marine ecosystems (Vitousek et al., 1997; Mack and D'Antonio, 1998; Pimentel et al., 2000). Non-native plant and animal species can be problematic in tidal saline wetlands (Strong and Ayres, 2013). In south Florida, there has been concern that two non-native mangrove species (*Brugeria gymnorrhiza* and *Lumnitzera racemosa*) introduced from the Indo-Pacific could spread from their current locations and become problematic invasive species that modify the structure and function of native mangrove forests (Fourqurean et al., 2010). In terrestrial ecosystems immediately upslope and adjacent to Gulf of Mexico mangrove forests, invasive non-native species are common and have altered the composition of many mangrove transitional communities. For example, in south Florida, *Schinus terebinthifolius* (Brazilian pepper tree), which was introduced in the early 1900s (Morton, 1978), has become one of the most problematic, non-native invasive plant species in the state (Ferriter, 1997). In certain areas, *S. terebinthifolius* has invaded mangroves and upslope

mangrove transitional areas (Ferriter, 1997; Ewe and Sternberg, 2007; Donnelly et al., 2008), which could affect the ability of mangrove forests to adapt to sea-level rise via horizontal movement along the landscape. *Casuarina equisetifolia* (Australian pine) and *Melaleuca quinquenervia* (Melaleuca) are two other problematic, non-native invasive plants that may affect landward migration of mangrove forests in Florida. In addition to plants, non-native animal species can also affect mangrove forests. For example, in south Texas, an introduced antelope from Asia (Nilgai; *Boselaphus tragocamelus*) (Leslie, 2016) eats *A. germinans* leaves (I. Feller, personal communication) (Day et al., 2018). And in the Everglades, the introduction and spread of the Burmese python, a non-native apex predator, has decimated mammal populations and altered trophic interactions in mangrove forests and the adjacent freshwater wetland ecosystems (Dorcas et al., 2012).

10. Land use change and anthropogenic drivers of loss

The drivers and rates of mangrove loss in the Gulf of Mexico have been country specific. In the United States, the primary drivers of mangrove loss and degradation have historically been coastal development (i.e., dredging and filling for urban or other land uses), drainage, and hydrologic impoundments (Johnston Jr, 1981; Lewis III et al., 1985; Dahl and Allord, 1996; Dahl, 2005; Lewis III et al., 2016; Thomas et al., 2017). In the late 1800s and early 1900s, mangrove forests and other wetland ecosystems in the United States were generally viewed by society in a negative light and targeted for drainage and conversion to other land uses (Mitsch and Gosselink, 2007). Some mangrove forests in Florida were converted directly to waterfront developments (Lewis III and Estevez, 1988; Lewis III and Robison, 1996), and others were drained via the use of linear canals in an effort to reduce mosquito populations (Smith et al., 2007). However, in the early 1970s, scientists across the world became increasingly aware of the many ecosystem goods and services provided by mangrove forests and other wetlands, and there was increasing public interest to protect wetlands. Since that time, various federal, state, and local regulations in the United States have been enacted and used to protect mangrove forests and other wetland ecosystems (Mitsch and Gosselink, 2007). Due in part to these regulations as well as concomitant wetland conservation efforts, the rate of mangrove forest loss due to direct conversion to other land uses has slowed considerably in the United States in recent decades (Dahl, 2005; Giri and Long, 2016).

In Cuba, mangrove loss and degradation have occurred primarily due to agricultural expansion, direct conversion to urban land uses, road and dam construction, and timber extraction (Milian Padrón, 1999; Lugo, 2002; Suman, 2003; Menéndez Carrera and Guzmán Menéndez, 2006; Rodríguez et al., 2006; Spalding et al., 2010; Menéndez Carrera, 2013; Suman, 2013; Blanco Rodríguez et al., 2014; Lugo et al., 2014). Estimates of the historical rates of mangrove loss in Cuba are highly variable (Friess and Webb, 2014). However, Suman (2013) indicates that the rate of mangrove loss in the previous several decades has likely decreased due to an increasing emphasis upon sustainable development, including mangrove protection, within Cuban environmental legislation and institutions. Nevertheless, mangrove loss due to coastal development continues to be a threat in Cuba (Menéndez Carrera, 2013), especially given anticipated future increases in coastal tourism and tourism-related infrastructure that could affect mangroves (Spalding et al., 2010; Suman, 2013; Lugo et al., 2014).

In Mexico, the primary drivers of mangrove loss have been agricultural activities, aquaculture, animal husbandry, and coastal development (López-Portillo and Ezcurra, 2002; Brusca et al., 2006; Spalding et al., 2010; Landgrave and Moreno-Casasola, 2012; Valderrama et al., 2014; Troche-Souza et al., 2016). Valderrama et al. (2014) and Troche-Souza et al. (2016) estimate that a 10% reduction in national mangrove coverage occurred between 1970 and 2005. Along the Gulf of Mexico coast, the Mexican states of Veracruz, Campeche, Yucatán, and Quintana Roo have had the highest mangrove losses during this period

Table 4
Potential strategies for conservation, restoration, and adaptation of mangrove forests in response to each of the nine global change drivers.

Global change driver	Strategies for conservation, restoration, and adaptation
↑ temperature	Protect and manage climatic refugia; Minimize non-native species introduction beyond natural range limits; Protect and manage hot spots for mangrove dispersal
↑↓ precipitation	Restore hydrologic connectivity; Manage freshwater inputs to maximize resistance and resilience to extremes; Target resistant species for restoration
↑ sea-level rise	Restore hydrologic connectivity; Protect and manage landward migration corridors; Maximize connectivity between ecosystems; Land acquisition
↑ tropical cyclone intensity	Future-focused land use planning; Mangrove restoration and creation; Protect and manage landward migration corridors; Maximize green infrastructure
↑ atmospheric carbon dioxide	Anticipate outcomes from altered biotic interactions; Maximize diversity to increase resistance and resilience
↑ land use change	Future-focused land use planning; Mangrove restoration and creation; Conservation easements; Payment for ecosystem services
↑↓ nutrient availability	Mangrove restoration and creation; Land use planning to manage anthropogenic nutrient inputs; Protect and manage connectivity to enable positive responses to nutrient alterations
↑ invasive non-native species	Anticipate and avoid novel introductions; Early eradication; Strategic management of established problematic species

(13%, 8%, 7%, and 5% decreases, respectively); in contrast, mangrove coverage in the states of Tabasco and Tamaulipas increased between 1970 and 2005 (7% and 16% increases, respectively) (Valderrama et al., 2014). Legislation in Mexico has increased the protection of mangrove forests and species, and since 2005, national mangrove coverage has been relatively stable (Troche-Souza et al., 2016). Nevertheless, like many parts of the world, there is continued pressure to convert mangrove forests in Mexico to other land uses including coastal development (Spalding et al., 2010; Environmental Law Institute and Centro Mexicano de Derecho Ambiental, 2011; Morzaria-Luna et al., 2014). Mangrove conversion to other land uses affects many ecosystem services including carbon storage and cycling. In an examination of the carbon implications of converting mangrove forest ecotones to cattle pastures in Tabasco and Campeche, Kauffman et al. (2016) show that mangrove conversion to other land uses results in large carbon losses and high greenhouse gas emissions. In Table 4, we present several strategies for using mangrove conservation and restoration to minimize global change impacts.

11. Interactions between global change drivers

In much of this review, we have evaluated the impacts of global change drivers independently. Most mangrove forests, however, have been or will be simultaneously affected by many different aspects of global change. In Table 1, we provide examples of the ecological consequences of interactions between global change drivers. A striking recent example comes from northern and western Australia, where recent mangrove diebacks were triggered by a combination of reduced precipitation, elevated temperatures, and lower sea levels (Duke et al., 2017; Lovelock et al., 2017). Another example comes from the northern Gulf of Mexico where landward and poleward expansion of mangroves is expected to occur in response to sea-level rise and less extreme winter air temperatures (Doyle et al., 2010; Osland et al., 2013). However, landward migration may also be hindered by coastal urban development, maladaptive freshwater management practices, drought, invasive species, or changes in nutrient availability. In the karstic region of the southern and southeastern Gulf of Mexico, sea-level rise, salinity changes, and tropical storm intensification may affect nutrient availability (McKee et al., 2002; Rivera-Monroy et al., 2011; Adame et al., 2013b). Elevated atmospheric carbon dioxide concentrations in all locations may modulate plant response to other global change drivers (McKee and Rooth, 2008; McKee et al., 2012; Saintilan and Rogers, 2015). While considering the independent effects of each global change factor provides an important foundation for considering and advancing understanding of global change impacts, comprehensive vulnerability assessments (sensu Glick et al., 2011) should ideally identify the global change drivers that may affect a particular mangrove forest and then evaluate the ecosystem's sensitivity, exposure, and adaptive capacity to the interactive effects of multiple global change drivers.

12. Challenges and opportunities for restoration, conservation, and adaptation

In the past century, the greatest threat to mangrove forests has been the direct conversion of mangrove forests to other land uses (Duke et al., 2007; Thomas et al., 2017). Along the Gulf of Mexico coast, various policies and legislation have been enacted in recent decades to protect and conserve mangrove forests. As a result, the rate of mangrove loss in the United States, Mexico, and Cuba is generally now lower than it was in the mid-to-late 20th century (Dahl, 2005; Suman, 2013; Valderrama et al., 2014; Giri and Long, 2016; Hamilton and Casey, 2016; Troche-Souza et al., 2016). Nevertheless, coastal cities and human populations continue to grow, and there is continued pressure to develop and convert valuable coastal wetland habitats like mangrove forests to other land uses (e.g., urban, aquacultural, or agricultural land uses) or to build infrastructure (e.g., roads, levees) that causes indirect damage. Hence, mangrove loss due to land use conversion does still occur and will continue to be a threat.

Where mangrove forests have been lost or degraded, mangrove restoration and creation efforts can help restore mangrove-derived ecosystem goods and services. With adequate resources, mangrove restoration is feasible and has a high potential for success once suitable tidal connectivity and inundation regimes have been established (Lewis III, 2005, 2009; Zaldívar-Jiménez et al., 2010; López-Portillo et al., 2017). In the United States, mangrove restoration efforts have become particularly common and successful in urban estuaries that have experienced high rates of mangrove loss. For example, mangrove forest losses in Tampa Bay and Miami-Dade County, Florida have been high due to direct conversion of mangrove forests during urbanization and coastal development (Lewis III and Estevez, 1988). In recent decades, public support and recognition of the value of mangrove forests has greatly increased, and local engineers and ecologists have developed significant local mangrove restoration expertise (Lewis III and Robison, 1996). In the past three decades, multiple large-scale mangrove restoration and creation efforts have been implemented across the Tampa Bay estuary and in Miami-Dade County, and these restoration efforts have provided many valuable ecosystem goods and services to the adjacent communities and the region (Proffitt and Devlin, 2005; Osland et al., 2012; Krauss et al., 2017). Mangrove restoration efforts in Cuba also have a long history, with some restoration sites in Habana dating back to the 1970s (Milian Padrón, 1996). In Mexico, mangrove restoration projects have been successfully implemented in several locations across the states of Veracruz, Campeche, and the Yucatán Peninsula (Zaldívar-Jiménez et al., 2010; López-Portillo et al., 2017).

In addition to efforts to protect and restore our existing mangrove forests, there is also a need for future-focused landscape conservation planning that will enable mangrove forests to adjust to the novel environmental conditions that are triggered by global change. In Table 4, we present potential conservation and restoration strategies that can be

used improve the adaptive capacity of mangrove forests to each of the nine global change drivers evaluated in this review. For example, in response to sea-level rise, mangroves are expected to migrate landward into upslope and upriver ecosystems (Williams et al., 1999; Doyle et al., 2010). In undeveloped coastal areas, landward mangrove migration into low-lying areas may be possible. However, in many urban estuaries, the landward migration of mangrove forests will be prevented by low-lying urban infrastructure (Titus, 1998; Titus and Richman, 2001; Scavia et al., 2002; National Research Council, 2007; Titus et al., 2009). In other words, developed areas, especially those protected by levees, dikes, and other coastal infrastructure, can serve as barriers that impede the landward migration of mangrove forests. Due to low-lying topography in the Gulf of Mexico region, there is much potential for wetland landward migration, particularly in Louisiana and Florida (Doyle et al., 2010; Enwright et al., 2016). However, urban and leveed barriers in certain areas (e.g., urban estuaries in Florida and leveed areas in Louisiana) are expected to prevent the landward migration of mangrove forests and other coastal wetlands (Erwin, 2009; Enwright et al., 2016; Borchert et al., 2018). To facilitate future landward migration of mangrove forests and maximize the mangrove-derived ecosystem goods and service available to future generations, conservation planning efforts should identify and protect upslope and upriver migration corridors.

Coastal wetland conservation efforts along the Gulf of Mexico will be affected by warming temperature regimes. For example, certain salt marshes and salt marsh-dependent ecosystem services in the northern Gulf of Mexico are particularly vulnerable to mangrove expansion. Although mangroves and salt marshes are both valuable ecosystems that each support important ecosystem goods and services, mangrove expansion will result in the gain of certain forest-dependent ecosystem services at the expense of other marsh-dependent ecosystem services (Osland et al., 2016; Kelleway et al., 2017). For salt marshes that are vulnerable to mangrove expansion, monitoring programs should be established to characterize the rate of forest encroachment. If the pace of mangrove expansion accelerates and important salt marsh habitat becomes compromised, it may be necessary to establish refugia for salt marsh ecosystems in the coldest coastal reaches in the region (i.e., Mississippi, Alabama, and northwest Florida).

The effects of altered rainfall and freshwater availability are expected to be particularly large along the driest coastal reaches in the region (i.e., near the United States-Mexico border and the Yucatán Peninsula). In these areas, mangrove forest stability can be enhanced via hydrologic restoration and by ensuring that adequate freshwater inputs (surface and ground water) and flow regimes are provided to mangrove forests. Inadequate freshwater inputs could exacerbate the combined ecological effects of drought (Osland et al., 2014b) and accelerated sea-level rise (Howard et al., 2017).

In this communication, we have attempted to demonstrate that interactions between multiple drivers can have large ecological consequences (Table 1), which can often exceed the independent effects of a single driver. Conservation strategies that seek to minimize the effects of interacting drivers will require a combination of approaches, some of which are identified in Table 4. For preparation and implementation purposes, managers often need to understand the timing of expected changes. While some of the global change effects described here may occur suddenly in an acute manner (e.g., mangrove mortality due to drought and hypersaline conditions, which may occur in a single year), other changes are expected to be more gradual due to chronic change (e.g., mangrove landward expansion and/or local loss in response to accelerated sea-level rise and coastal squeeze). Nevertheless, these changes evaluated in this communication are expected to accelerate in the coming decades (USGCRP, 2017). Hence, there is a pressing need for future-focused management efforts that can maximize the ability of mangrove forests to adapt to future change.

13. Conclusions

(1) The climatic gradients present along the Gulf of Mexico make it a particularly valuable region for investigations of climate change impacts to mangrove forests. Along the northern Gulf of Mexico coast, future changes in the intensity, duration, and frequency of winter air temperature extremes are expected to enable mangrove forests to expand northward at the expense of salt marshes. In the coming century, changing precipitation, hydrologic, and estuarine salinity regimes are expected to affect certain mangrove forests along the Gulf of Mexico coast as well as those present along arid and semi-arid coasts across the world. Coastal wetlands in arid and semi-arid climates are particularly sensitive to small changes in freshwater availability, which can trigger comparatively large changes in mangrove coverage, structure, and function. In these regions, the effects of drought and changing precipitation regimes can be minimized by ensuring that adequate freshwater flow regimes are provided to estuaries.

(2) In addition to climatic gradients, Gulf of Mexico wetlands span a wide range of geomorphic gradients that modulate wetland responses to sea-level rise. Mangrove forests in the region are located in large sediment-dependent deltas and also along karst-dominated and sediment-poor oligotrophic coasts. Accelerated sea-level rise is expected to have a particularly large effect on mangrove forests by modifying inundation and salinity regimes, which greatly influence mangrove ecosystem structure and function. For example, near the mangrove-open water ecotone, small increases in sea level rise can result in the submergence and loss of mangrove forests. Conversely, at higher elevations, small changes in sea level can prompt the landward migration of mangrove forests at the expense of upslope or upriver ecosystems. To persist during sea-level fluctuations, mangrove forests must adjust their vertical and/or horizontal position in the landscape. Across the Gulf of Mexico, there is a need for future-focused landscape conservation efforts that will facilitate the migration of mangrove forests into upslope and upriver ecosystems in response to accelerated sea-level rise.

(3) Mangrove forests are threatened by many different aspects of global change, and the interactive effects of certain global change drivers can transform mangrove forests and even lead to mangrove mortality. We provide examples of the potential ecological consequences of interactions between global change drivers (i.e., temperature change, precipitation change, accelerated sea-level rise, tropical cyclone intensification, elevated carbon dioxide, land use change, eutrophication, and invasive non-native species) (Table 1).

(4) We live in an era of rapid and unprecedented ecological change. Although mangrove forests are highly resilient ecosystems that have some capacity to adapt and adjust to changing conditions, mangrove forests are also highly vulnerable to the interactive effects of global change. To ensure that the ecosystem goods and services provided by mangrove forests continue to be available for future generations, there is a pressing need to better protect, manage, and restore mangrove forests as well as the adjacent ecosystems that provide opportunities for adaptation in response to global change.

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